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MICROHABITAT USE BY BREEDING SOUTHWESTERN WILLOW FLYCATCHERS ON THE GILA RIVER, NEW MEXICO

SCOTT H. STOLESON AND DEBORAH M. FINCH

Abstract. The endangered Southwestern Willow Flycatcher (Empidonax traillii extimus) breeds at numerous sites throughout its range that vary greatly in floristics, vegetation structure, and the extent of human alteration of the habitat. Here we present information on nesting habitat characteristics of Willow Flycatchers in the largest extant population of the subspecies along the upper Gila River in New Mexico. We compared 19 habitat variables between nest sites and sites not included in flycatcher territories. A logistic regression model identified three variables as significant predictors of flycatcher use: foliage density in the subcanopy, percent canopy cover, and number of boxelder (Acer negundo) stems. In mature riparian woodland, flycatchers displayed a significant preference for nesting in boxelder, and used two willow species less than expected by chance. Flycatchers in the Gila Valley tended to place nests rather high (mean = 7.6 m). The relative nest height, preference for dense foliage, and proximity to water were typical for the subspecies.

Key Words: Cliff-Gila Valley; Empidonax traillii extimus; habitat selection; nest site; New Mexico; Southwestern Willow Flycatcher.

Habitat structure and floristics can strongly affect the distribution and productivity of birds (Martin and Roper 1988, Block and Brennan 1993, Martin 1998). For endangered bird species, recovery often depends on identifying, preserving, and possibly restoring suitable habitat. A clear understanding of what comprises suitable habitat is especially important when habitat loss constitutes the primary cause of a species' decline or when a species has narrow habitat preferences.

The Southwestern Willow Flycatcher (Empidonax traillii extimus) is a riparian obligate inhabiting dense streamside thickets and woodland (Sedgwick 2000, Sogge and Marshall 2000). In the past century, most of the riparian habitat in the Southwest has been destroyed or degraded due to urban and agricultural development, water management, channelization, overgrazing, recreation, and invasion by exotic saltcedar (Tamarix ramosissima; Patten 1998, Cartron et al. 2000, Marshall and Stoleson 2000). The Southwestern Willow Flycatcher has shown a concomitant decline (Unitt 1987), resulting in it being listed as an endangered species in 1995 (U.S. Fish and Wildlife Service 1995). The most recent population estimates total 986 known territories rangewide (Sogge et al. this volume).

Recovery of this endangered subspecies will depend on the identification of preferred habitat as targets for preservation and as goals for restoration. A clear, quantitative understanding of what constitutes preferred habitat has been hindered by the fact that occupied sites vary greatly in floristics and vegetation structure (Sogge and Marshall 2000). Currently, flycatchers breed in numerous altered or degraded sites, including many dominated by exotic saltcedar (Paradzick

et al. 1999, U.S. Fish and Wildlife Service 2001).

We describe the nest site and nesting microhabitat characteristics of a population of Willow Flycatchers along the upper Gila River in New Mexico. This valley supports the largest known breeding concentration of E. t. extimus (estimated at 243 pairs in 1999; S. Stoleson and D. Finch, unpubl. data). Birds in this population exhibit nest site and microhabitat characteristics that differ in some respects from those reported elsewhere (Stoleson and Finch 1999b, Sedgwick 2000, Sogge and Marshall 2000). Information on nest site preferences for this population has previously been reported only in unpublished reports (e.g., Skaggs 1996). The data presented here should help to provide a more complete picture of the habitats used by breeding Willow Flycatchers in the Southwest and provide insights into important habitat components.

METHODS

STUDY SITE

This study was conducted in the Cliff-Gila Valley of Grant County, New Mexico, (32° 58' N, 108° 34' W) in 1997-2000. Most of this broad floodplain is private land (the U Bar Ranch) consisting of irrigated and dry pastures used for livestock grazing and hay farming. Adjacent areas include protected lands of The Nature Conservancy and the Gila National Forest. Elevations range from 1335 to 1420 m. The Gila River and nearby earthen irrigation ditches are lined with riparian woodland patches of various ages and composition. Most patches support a mature woodland (>25 m canopy) composed primarily of Fremont cottonwood (Populus fremontii), Goodding's willow (Salix gooddingii), boxelder (Acer negundo), velvet ash (Fraxinus velutinus), Arizona walnut (Juglans major), Arizona sycamore (Platanus wrightii), Arizona alder (Alnus oblongifolia), and Russian olive (Elaeagnus angustifolia). The understory is composed of shrubs including three-leaf sumac (Rhus trilobata), false indigo (Amorpha fruticosa), New Mexico olive (Forestieria neomexicana), forbs, and grasses. Fewer patches support a shrubby, early successional growth of seepwillow (Baccharis glutinosa), coyote and bluestem willows (Salix exigua and S. irrorata), and saplings of the species mentioned above. Most habitat patches are less than 5 ha in area, and the total area of riparian woodland included in this study is approximately 75 ha.

FIELD METHODS

We searched for nests in occupied patches daily throughout the breeding seasons (May–Aug.) of 1997–2000 during spot-mapping censuses, area searches, and focused nest searches (Martin and Geupel 1993). We found nests in approximately 70–85% of territories each year, based on spot-mapping data. At each nest, we recorded tree species, height, and diameter, and nest height. We also calculated the relative height of nests as nest height/nest tree height. We identified the dominant tree for nest sites where one tree species made up ≥50% of stems within 8 m of the nest. All vegetation measurements were performed after fly-catcher breeding activity in the area had ceased (27 Jul–3 Sept).

Within occupied patches, we sampled microhabitat characteristics at 127 nest sites and 89 randomly selected non-use sites using a modified BBIRD methodology (Martin et al. 1997). Vegetation at nest sites was measured in a sample plot centered on the nest tree (see below). Southwestern Willow Flycatchers at this site often reused nest trees within and among years, and resighting of color-banded individuals suggests a high degree of site fidelity (S. Stoleson and D. Finch, unpubl. data). We also detected no significant yearly variation in habitat preferences (variables in Table 2, ANOVA, all P > 0.29). Thus, to avoid any problems of non-independence, we took a conservative approach and included in analyses only nest plots with no spatial (8-m radius) overlap within or among years. Non-use sites were randomly selected from points on spot-mapping grids that were at least 33.5 m away from the nearest Willow Flycatcher nest, as most flycatcher territories at this site appeared to have radii much smaller than 33.5 m (S. Stoleson and D. Finch, unpubl. data). We assumed that all riparian habitat within spot-mapping grids was available to arriving flycatchers to set up territories.

At each nest and non-use site, we established a 0.02ha circular sample plot (radius = 8 m). Sample plots at non-use sites were centered on the closest tree to the spot-map grid point. At the center of the plot and at eight other points (4 and 8 m from the center in each of the four cardinal directions), we measured canopy height using clinometers, percent canopy cover using densiometers, and estimated percent ground cover. Vertical foliage density was measured at 2, 4, 6 and 8 m from the center tree in each cardinal direction by counting hits of vegetation against a 10-m vertical pole marked in 1-m increments. We recorded the number and size class (dbh) of all trees (≥10 cm dbh) within the 8-m radius plot, and the number and size class of shrubs and saplings (<10 cm dbh) within a 4-m radius of the center tree.

For each sample plot, we calculated average ground and canopy cover and average canopy height (mean of 9 measurements per plot); foliage density index (count of 1-m increments touched by foliage) for understory (0-3 m in height, for a maximum score of 48 per plot) and mid-canopy (3-10 m in height, for a maximum score of 112 per plot); and the sum of shrub/sapling (<10 cm diam) stems and tree (≥10 cm diam) stems by species and size class (<1 cm, 1-4.9 cm, 5-7.4 cm, 7.5-9.9 cm, 10-29.9 cm, 30-49.9 cm, 50-70 cm, >70cm). From these values we also calculated the total number of stems of each woody plant species per plot, an estimate of the total basal area of woody species per plot, woody plant species richness (number of species of trees and shrubs per plot), and plant species diversity (using the Shannon diversity index). We calculated several variables to estimate the degree of habitat heterogeneity within each sample plot: patchiness (the Shannon diversity index of total foliage density among the four cardinal directions); and the coefficient of variation in measures of canopy cover, canopy height, and ground cover within each plot. We also measured horizontal distance from each sample plot center to the closest surface water and closest edge of the habitat patch.

We compared habitat values between non-use sites and nest sites using either independent sample t-tests when data were normally distributed or could be normalized through standard transformations, or Mann-Whitney U-tests when data could not be normalized. Habitat variables found to differ significantly (using Bonferroni's adjustment for multiple tests on a single data set; Rice 1989) between nest and non-use sites were included in a logistic regression model (Menard 1995). We used a value of $P \le 0.10$ to enter and \ge 0.05 to remove individual variables from the model. We chose the most parsimonious logistic regression model with equal numbers of parameters using Akaike's Information Criterion (AIC) and used likelihoodratio chi-square tests to test for significant effects between nested models (Anderson et al. 2000). We compared the likelihood of occurrence of the six most frequent herbaceous groundcovers between nest and non-use sites using chi-square analyses. All means are presented ± 1 sp.

We also tested the hypothesis that Southwestern Willow Flycatchers chose nest trees randomly by comparing tree species usage with availability. Flycatcher nests were found in vegetation of all size classes ≥1 cm diameter, so we considered all stems in these classes as potential nest substrates. A composite stem count for each species was calculated from all nest plots. We assumed counts of stems at ground level were representative of the relative abundances of tree species available to flycatchers for nest placement. For each tree species we compared the (arcsine-transformed) proportion of stems used for nesting with their relative availability (proportion of all stems) using chisquare analyses.

RESULTS

NEST SUBSTRATES

We located a total of 488 Southwestern Willow Flycatcher nests. The majority (76%) of

TABLE 1. WILLOW FLYCATCHER NEST SUBSTRATES AND HEIGHTS IN THE CLIFF-GILA VALLEY, 1997–2000

					Nest heights		
Plant species	No. (%) nests		No. (%) stems		Mean	SD	Range
Boxelder	371	(76.0)	2188	(43.3)	8.4	3.4	1.8–19.0
Goodding's willow	36	(7.4)	1007	(19.9)	4.6	2.6	1.7-13.2
Fremont cottonwood	22	(4.5)	150	(3.0)	7.2	4.8	2.0 - 24.1
Russian olive	19	(3.9)	197	(3.9)	4.3	1.9	1.0 - 8.0
Coyote willow	15	(3.1)	857	(16.9)	2.6	0.9	1.5 - 4.2
Arizona alder	13	(2.7)	132	(2.6)	6.3	2.5	2.3 - 10.0
Saltcedar	4	(0.8)	25	(0.5)	2.7	0.5	1.9 - 3.1
Seepwillow	3	(0.6)	131	(2.6)	2.0	0.1	1.9 - 2.0
Arizona sycamore	2	(0.4)	18	(0.3)	11.0	4.2	8.0-14.0
Rose (Rosa multiflora)	1	(0.2)	2	(<0.1)	4.0		
Canyon grape (Vitis arizonica)	1	(0.2)	34	(0.7)	1.5		
Siberian elm (Ulmus pumila)	1	(0.2)	27	(0.5)	3.6		
Total/mean	488	(100.0)	5058	$(94.3)^{a}$	7.6	3.7	1.0-24.1

^a Figure does not total to 100% because it omits plant species not used by flycatchers for nesting.

these were placed in boxelder trees. Goodding's willow was the second most frequent nesting substrate (7% of nests), with the remaining nests found in ten other plant species (Table 1). In the Cliff-Gila Valley, flycatchers placed nests in cottonwood and seepwillow only in young stands.

Flycatchers did not select nest tree species in proportion to their availability ($\chi^2 = 26.4$, df = 4, P < 0.01; Table 1). Boxelder was used significantly more than would be expected if birds chose nest trees randomly ($\chi^2 = 22.6$, df = 1, P < 0.01). It comprised 43% of the woody stems over 1 cm diam, yet contained 76% of all nests. In contrast, Goodding's willow was used less than expected by chance ($\chi^2 = 6.4$, df = 1, P = 0.01); it comprised almost 20% of all stems but was used for less than 8% of nests. Coyote willow was also used less than expected ($\chi^2 = 10.7$, df = 1, P < 0.01). Other substrates were used too infrequently for meaningful comparisons of use versus availability (Table 1).

Willow Flycatchers tended to build nests in the numerically dominant woody plant species within nest plots; 81% were placed in the most frequent tree species within the plot. Flycatchers placed nests in boxelder at 139 of 141 (99%) nest sites dominated by boxelder. However, they also placed nests in boxelder in 4 of the 16 nest sites dominated by Goodding's willow and in over a third (36%) of the 39 nest sites dominated by species other than boxelder, either willow, or Russian olive.

NEST HEIGHTS

The mean height of all nests found was 7.6 ± 3.7 m, with a median height of 7.0 m (range 1.0-24.1 m; Table 1). Heights varied considerably among different nesting substrates (Table 1). Boxelder nests were significantly higher (8.4)

 \pm 3.4 m) than nests in all other substrates combined (mean = 4.9 \pm 3.3 m; t = -10.6, df = 202.9, P < 0.01). Nest trees averaged 12.3 \pm 5.0 m tall (range 2.2-27.0 m), with diameter of 22.4 \pm 16.7 cm (range 0.5-142.7 cm). The relative height of Willow Flycatcher nests within nest trees averaged 0.62 \pm 0.17.

MICROHABITAT OF NEST VS. NON-USE SITES

Microhabitat around nest sites differed substantially from that at non-use sites. In univariate comparisons, 9 of 19 habitat variables differed significantly (P < 0.01) between nest and nonuse sites (Table 2). Nest sites typically had less ground cover, greater canopy cover that was less variable, greater foliage density between 3 and 10 m, greater foliage density patchiness, more trees and boxelder stems, and fewer stems of cottonwood (Table 2). Logistic regression analysis identified three of these variables as significant predictors of flycatcher nesting. The best model was logit (p) = -10.69 + 0.09 (subcanopy foliage density) + 0.28 (% boxelder stems) + 0.09 (mean canopy cover). The likelihood of a site being used for nesting by flycatchers increased with greater foliage density, greater proportion of boxelder, and greater mean canopy cover.

Used sites also differed from non-use sites in the occurrence of certain species of common understory herbaceous plants. Nest sites were significantly more likely to have wetland forbs such as spearmint (*Mentha spicata*; $\chi^2 = 4.4$, df = 1, P = 0.03) and nettles (*Urtica dioica*; $\chi^2 = 9.0$, df = 1, P < 0.01). In contrast, non-use sites were significantly more likely to have horehound (*Marrubium vulgare*; $\chi^2 = 5.3$, df = 1, P = 0.02), four o'clocks (*Mirabilis* spp.; $\chi^2 = 16.8$, df = 1, P < 0.01), jimsonweed (*Datura*

TABLE 2. Univariate Comparisons of Continuous Habitat Variables Between Willow Flycatcher Nest Sites and Non-use Sites

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Variable	Nest sites $(N = 127)$	Non-use sites $(N = 89)$	Test statistic ^a	df	Pb
Average ground cover (%)	30.0 ± 23.4	39.2 ± 19.3	t = 3.17	208.4	< 0.01
CV ground cover	1.0 ± 0.5	0.7 ± 0.4	t = 1.28	214	0.20
Average canopy cover (m)	88.7 ± 7.9	78.8 ± 12.4	U = 2641.0		< 0.01
CV canopy cover	0.1 ± 0.1	0.2 ± 0.2	U = 4952.0		< 0.01
Average canopy height (m)	13.9 ± 4.7	17.4 ± 9.7	t = -0.22	150.5	0.83
CV canopy height	0.3 ± 0.2	0.4 ± 0.3	t = 2.46	135.5	0.02
Foliage density 1-3 m	12.2 ± 6.6	13.8 ± 6.3	t = 2.87	214	0.01
Foliage density 3–10 m	41.7 ± 12.6	25.9 ± 13.7	t = -8.76	214	< 0.01
Foliage height diversity	1.5 ± 0.2	1.1 ± 0.2	t = -2.42	157.9	0.02
Foliage density patchiness	1.34 ± 0.05	1.29 ± 0.13	U = 3573.0		< 0.01
Total of shrub stems (<10 cm)	29.3 ± 44.5	19.7 ± 25.6	U = 5535.0		0.01
Total of tree stems (≥10 cm)	9.8 ± 4.7	5.8 ± 3.6	t = -4.69	146.1	< 0.01
Total of boxelder stems	6.0 ± 4.1	1.6 ± 2.6	t = -6.10	214	< 0.01
Total of willow stems	9.9 ± 37.9	3.7 ± 8.0	U = 8023.0		0.61
Total of cottonwood stems	0.5 ± 1.7	1.6 ± 3.4	U = 6911.0		< 0.01
Plant species diversity	0.6 ± 0.5	0.7 ± 0.5	t = 1.26	214	0.21
No. of woody plant species	3.0 ± 1.7	2.9 ± 1.5	t = -0.28	214	0.78
Distance to nearest water (m)	41.2 ± 53.8	63.0 ± 58.9	t = 2.83	214	< 0.01
Distance to nearest edge (m)	9.9 ± 8.6	9.7 ± 7.0	t = -0.18	423	0.86

a t-tests when data met assumptions of normality, Mann-Whitney U-tests when data could not be normalized.

b P-values in boldface were statistically significant based on Bonferroni's correction for experiment-wise error rate (Rice 1989).

wrightii; $\chi^2 = 6.0$, df = 1, P = 0.02) and morning glories (*Convolvulus* spp.; $\chi^2 = 28.4$, df = 1, P < 0.01).

DISCUSSION

NEST SITES

Southwestern Willow Flycatchers in the upper Gila River Valley of New Mexico differed from other known populations both in the high average placement of their nests and in the predominant nesting substrate (Sedgwick 2000, Sogge 2000b). The high use of boxelder appears to be unique to this population. This likely reflects the fact that in the Southwest, boxelder occurs primarily above 1200 m elevation, higher than most sites occupied by Southwestern Willow Flycatchers (Boles and Dick-Peddie 1983, Szaro 1989, U.S. Fish and Wildlife Service 2001). Unlike many other areas of the Southwest, where willows tend to dominate riparian areas, flycatchers in the Cliff-Gila Valley underutilized willows as nesting substrates (Szaro 1989, Sogge 2000b, U.S. Fish and Wildlife Service 2001). Our findings are congruent with those of Mc-Cabe (1991:49) from his study of E. t. traillii in Wisconsin, in which he suggested that where the bird has a choice of willows or other substrates, willow tends not to be preferred. The relatively frequent use of exotic Russian olive in this mostly native habitat is noteworthy in light of its encroachment into riparian habitats in the region (Olson and Knopf 1986).

Our results suggest potential working hypotheses to test whether the apparent habitat preferences reported here confer fitness benefits to breeding flycatchers, perhaps through reduced vulnerability to predation or brood parasitism by Brown-headed Cowbirds (Molothrus ater). Boxelder may provide such potential benefits simply because flycatchers nest higher than in other substrates. The likelihood of brood parasitism was inversely correlated with nest height in the closely related Least Flycatcher (Empidonax minimus; Briskie et al. 1990). In this population, rates of brood parasitism were significantly lower in boxelder than in Russian olive, even when nest height and distance from edge were controlled for (S. Stoleson and D. Finch, unpubl. data), suggesting possible benefits from boxelder not related to nest height. Our results also suggest that riparian restoration in the Southwest need not be focused solely on willows to provide suitable habitat for flycatchers; planting of boxelder may be appropriate in some middle and upper-elevation areas.

In the Cliff-Gila Valley, Willow Flycatchers tended to nest considerably higher than in all other known populations (Sedgwick 2000). However, the high placement of nests was not uniform at our site. Birds placed nests unusually high in boxelder, cottonwood, alder and sycamore (Table 1). Mean nest height in willow (4.0 m) and saltcedar (2.7 m) was similar to nests in those trees elsewhere in the Southwest (Sogge

2000b). Although absolute heights of Willow Flycatcher nests in the Cliff-Gila Valley were unusually high, the relative position of those nests within the nest tree was very typical. The mean relative height here (0.62) was very similar to that reported by McCabe (1991) for his shrub-inhabiting *E. t. traillii* population (0.62, N = 601 nests). Similarly, the mean relative nest height in Arizona (based on mean values for nest and tree heights for nests located in 2000) was 0.60 (N = 202; Paradzick et al. 1999). This suggests nest placement by flycatchers may be based on relative position within the nest tree, and absolute height may simply reflect the stature of the habitat.

HABITAT PREFERENCES

The only significant predictors of flycatcher use indicated by logistic regression were foliage density in the subcanopy, number of boxelder stems, and average canopy cover. This suggests flycatchers may preferentially establish territories in dense, shady thickets of boxelder, their preferred nest tree in this habitat. Univariate comparisons indicated that flycatchers also tended to settle near water and where foliage was heterogeneous. Except for the boxelder, these results are congruent with descriptions of Willow Flycatcher nesting habitat elsewhere in the West (Whitmore 1977, Flett and Sanders 1987, Sedgwick and Knopf 1992, Sogge et al. 1997b). Our results should be combined with similar habitat assessments conducted elsewhere in the range of E. t. extimus in a meta-analysis (Arnqvist and Wooster 1995) to develop a comprehensive, quantitative habitat model for the subspecies.

Although almost half of the habitat variables examined differed significantly between nest sites and non-use sites, only three were signifi-

cant predictors of flycatcher use. There are several possible explanations for this lack of discriminatory power. Our assessment was based on, and measured around, nest sites, but avian territories serve additional functions including providing song perches and an adequate food base (Prescott and Middleton 1988, Sedgwick and Knopf 1992). Our methods may have assessed correlates of these other functions only poorly. Alternatively, settlement patterns of flycatchers may be more closely associated with habitat features at larger spatial scales, such as patch or watershed (Freemark et al. 1995, Saab 1999). Within New Mexico's Gila Valley, numerous areas of riparian habitat remain unoccupied by Southwestern Willow Flycatchers (S. Stoleson and D. Finch, unpubl. data). These patterns may reflect habitat preferences of the flycatcher at the patch and landscape scales; suitable microhabitat may exist in unsuitable landscapes. Alternatively, there may be too few flycatchers to saturate the area. Future research should concentrate on identifying patterns of flycatcher habitat selection at these larger spatial scales.

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